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Introduction

Hypera postica Gyllenhal (Coleoptera: Curculionidae) is an introduced insect pest from Central Asia, and was first discovered in the United States (Utah) in 1904 (Dysart & Day 1976). It was first reported in the Eastern U.S. in 1951, and in Iowa in 1967 (Armbrust et al. 1970, Stockdale 1967). *H. postica* increased dramatically in the absence of its native natural enemies, and caused widespread economic losses throughout the Eastern U.S. (Day 1981, Wintersteen 1992). In 1957, the USDA began importing and releasing parasitoid wasps to reduce weevil populations. These natural enemies reduced populations of *H. postica* and saved east coast alfalfa growers $8 million dollars each year in reduced insecticide use and alfalfa damage (Day 1981, Wintersteen 1992). In an economic analysis of the alfalfa weevil biological control program, Moffit et al. (1990) concluded that the benefits of this program for the entire U. S. are equivalent to $88 million dollars per year (1987 dollars).

In addition to these beneficial wasps, a weevil specific fungus, *Zoophthora phytonomi* (Entomophthorales: Entomophthoraceae), attacks and kills *H. postica* larvae and pupa, occasionally causing mortality greater than 90% (Giles et al. in press, Harcourt et al. 1990). Since its first report in Ontario in 1974, *Z. phytonomi* has spread naturally to alfalfa growing regions throughout most of the United States (Harcourt et al. 1974, Burger & Bryan 1991). Epizootics (outbreaks of disease) usually begin during humid conditions on peak densities of alfalfa weevil larvae and continue over a 2-week period (Harcourt et al. 1990). *Z. phytonomi* was first detected in Iowa during the spring of 1982; Carl Carlson reported that 13% of the *H. postica* larvae collected in Story and Boone Counties were infected by the fungus (Sweets 1982).

From 1975-1987, several alfalfa weevil parasitoids were mass reared from established U.S. colonies and released in Iowa (Burger & Bryan 1991). These included the following parasitoids that attack different life stages of the weevil:

Larval Parasitoids *Bathyplectes anurus* Thomson (Ichneumonidae)
Tetrastichus incertus Ratzburg (Eulophidae)

Pupal Parasitoid *Dibrachoides dynastes* Foerster (Pteromalidae)

Adult Parasitoids *Microctonus colesi* Drea (Braconidae)
M. aethiopoides Loan (Braconidae)

In addition to these released species, the larval parasitoid *Bathyplectes curculionis* Thomson (Ichneumonidae), introduced into the U.S., has spread on its own throughout much of the country including Iowa (Burger & Bryan 1991).

Results of Parasitoid Releases in Iowa

During the 1980's, after mass releases of these parasitoids, alfalfa weevil populations declined in Iowa. In southern Iowa from 1981-1987, a negative correlation was observed between adult weevil densities and percent parasitism (Kingsley et al. 1993, in press). In 1983, *M. aethiopoides* parasitized 41.5% of *H. postica* adults collected in central Iowa (Mertins 1984).

In 1989, however, larval populations reached economic densities in southern Iowa and required insecticide applications (Rice 1989). This outbreak of *H. postica*, following a period when established natural enemies effectively reduced weevil populations, was not understood. Why didn't established parasitoids and the fungal pathogen prevent the outbreak? Was the pathogen reducing the effectiveness of the parasitoids? Only a quantitative evaluation of these natural enemies could answer these questions.

Monitoring *H. postica* Natural Enemies in Iowa

In 1990, the Alfalfa IPM Interdisciplinary Research Team, funded by the Leopold Center for Sustainable Agriculture, initiated research with the long term objectives of: (1) integrating biological, cultural, and chemical controls, as well as, interactions of diverse pest complexes (insects, pathogens, and weeds) into IPM decision models, and (2) to deliver environmentally and economically sound IPM systems for sustainable agricultural systems in Iowa. One component of this research was to document the seasonal occurrence and impact of predators, parasitoids, and pathogens attacking *H. postica* larvae in northeastern, central, and south-central Iowa. The interactions among observed biotic mortality factors (*Z. phytonomi*, *B. anurus*, and *B. curculionis*) and the effect of abiotic factors (temperature and moisture) on host density and the phenology of *Z. phytonomi* were also quantified.

Parasitoid-Pathogen Study

In 1990, 1991, and 1992 alfalfa weevil larval populations were monitored throughout the spring by stem (Guppy et al. 1975, Harcourt et al. 1977) and sweep samples from 30 March to 26 June, or until first harvest, in eight Iowa counties. Galen Eiben (Wartburg College) and Ken Nuss (University of Northern Iowa) sampled populations in Bremer, Fayette, Clayton, and Butler Counties. Larvae were sampled in Story, Polk, Marion, and Lucas Counties by Kristopher Giles (Iowa State University) and Todd DeGooyer (Iowa State University). *H. postica* larvae were collected from each site and reared individually on alfalfa terminals until pupation, parasitoid emergence, or death. Percentage mortality from parasitoids and *Z. phytonomi* were calculated by dividing the number of parasitized or diseased larvae by the total number of *H. postica* larvae collected on each sampling date. Larval populations (Larvae per stem) were estimated on each sampling date by stem sampling, and larval extraction using modified Berlese funnels (DeGooyer 1993, Guppy et al. 1975). Daily rainfall, and degree day accumulations above 9°C (48°F) after 1 January were calculated at each location using maximum and minimum air temperatures (Wedberg et al. 1980, Iowa Climate Review 1990, 1991, 1992). For more detailed information on sampling procedures and methodology, see Giles (1992) and DeGooyer (1993).

Predators of Alfalfa Weevil Larvae

Alfalfa sampling for predators was conducted weekly in Story, Polk, Marion, and Lucas County alfalfa fields in 1991 and 1992. Fields used were the same as in the parasitoid-pathogen study. Weekly sampling began on 16 April and continued through 7 June. In each field, a 49 x 49 m area was sampled along four parallel transects for predators and prey. Four 100 sweep sampling units were taken along each transect using standard canvas sweeping nets (38 cm in diameter). Each unit was emptied into a plastic bag, transported to the laboratory, frozen, and sorted.

To determine if predators aggregate to varying prey densities, the total numbers per 100 sweeps were calculated for the following prey and predator categories. Prey categories consisted of *H. postica* larvae and the pea aphid *Acyrthosiphon pisum* (Homoptera: Aphididae), two highly abundant phytophagous insect species found on alfalfa in Iowa. Predator categories included representatives from the Coleoptera (Coccinellidae) and Hemiptera (Nabidae and Pentatomidae) that are commonly observed feeding on *H. postica* and *A. pisum* . *Coleomegilla maculata* (Coleoptera: Coccinellidae) adults were recorded as a separate predator category because of their abundance in Iowa. Details on methodology and data analysis can be found in Giles (1992).

Results and Discussion

Larval Parasitism

In 1990, 5% of the larvae collected in Bremer County were parasitized by *Bathyplectes curculionis*. *B. curculionis* was the most abundant larval parasitoid in Marion County, accounting for 65% of larval parasitism. Thirteen percent of the larvae were parasitized by *B. anurus* (Table 1), whereas 22% of the parasitoid larvae emerging from *H. postica* larvae did not spin cocoons, and died. In Lucas County (1990) parasitism by *B. curculionis* and *B. anurus* peaked in May at 12% (245 Degree Days (DD)), declining to 3.4% (282 DD) at the time of harvest. *B. curculionis* was the most abundant larval parasitoid in Lucas County (Table 1). Twenty four percent of the parasitoid larvae emerging from *H. postica* larvae did not spin cocoons, and died.

In 1991, no parasitoids were recovered in Bremer, Fayette, Clayton, and Butler Counties. Peak larval parasitism at each central and southcentral Iowa location was: Story - 15% (198 DD), Polk - 14% (166 DD), Marion - 40% (247 DD), Lucas - 44% (195 DD). In 1992, peak larval parasitism in northeastern Iowa counties were: Bremer - 14%, Fayette - 18%, Clayton - 9%, Butler - 10%. Peak larval parasitism in 1992 at each central and southcentral Iowa location was: Story - 8% (292 DD), Polk - 4% (206 DD), Marion - 28% (283 DD), Lucas - 37% (178 DD).

In 1992, *B. anurus* represented 74% of the recovered parasitoids from Bremer, Fayette, Clayton, and Butler Counties combined. From 1991 to 1992, *B. anurus* represented between 59-80% of the recovered parasitoids from Marion and Lucas Counties (Table 1). Unidentified larval parasitoids (PA?) represented from 6-16% of the recovered parasitoids in Marion and Lucas Counties in 1991 and 1992 (Table 1). In Story County where levels of parasitism were relatively low, *B. curculionis* was the most abundant parasitoid in 1991 (6.2%) and 1992 (2.2%).

Disease - Influence of Rainfall and Alfalfa Weevil Densities

Rainfall appears to be a major environmental factor influencing the initiation and spread of *Z. phytonomi* infections on *H. postica* larval populations in Iowa. In each of the northeast Iowa counties, larval populations were reduced to near zero by *Z. phytonomi* from 22 to 29 May during periods of above average rainfall. In central and southcentral Iowa, first incidence of *Z. phytonomi* varied greatly between 1991 and 1992 at each sampling site. Compared with 1992, disease occurred from 70-177 DD earlier in 1991 (Table 2). In 1991, first incidence of *Z. phytonomi* occurred after an average of 179 DD (>9°C). This relatively early incidence may be the result of above average rainfall levels that occurred at each location in 1991 (Table 2).

In addition, early initiation coupled with continuing high rainfall, enhanced the spread of disease on low larval densities in 1991 resulting in high peak mortality (Table 2). Six epizootics (>50% host infection) were observed in central and southcentral Iowa during this three year

Table 1. Yearly totals and percentages of mortality from naturally occurring biological control agents of *Hypera postica* larvae at four locations in Iowa, 1990-1992

Location	H. postica[a]	B.a.[b]	B.c.[c]	PA?[d]	% PA[e]	Z.p.[f]
			1990			
Marion Co.	457	12	63	17	20.1	68 (14.9)
Lucas Co.	582	14	24	12	8.6	71 (12.2)
			1991			
Location	H. postica	B.a.	B.c.	PA?	% PA	Z.p.
Story Co.	275	4	11	2	6.2	131 (47.6)
Polk Co.	221	5	4	0	4.1	135 (61.1)
Marion Co.	319	34	18	6	18.2	156 (48.9)
Lucas Co.	407	64	12	6	20.1	60 (14.7)
			1992			
Location	H. postica	B.a.	B.c.	PA?	% PA	Z.p.
Story Co.	364	2	5	1	2.2	117 (32.1)
Polk Co.	501	5	6	2	2.6	57 (11.4)
Marion Co.	251	31	10	4	17.9	2 (0.8)
Lucas Co.	272	60	3	12	27.6	23 (8.5)

[a], H. postica is the number of *H. postica* larvae reared each year from each site.

[b], B.a. is the number of *B. anuraus* reared.

[c], B.c. is the number of *B. curculionis* reared.

[d], PA? is the number of parastoid larvae that did not spin species distinct cocoon.

[e], %PA is the seasonal percentage parasitism (B.c., B.a., and PA?).

[f], Z.p. is the number and percentage (%) of *H. postica* larvae infected with *Z. phytonomi*.

From Giles, 1992

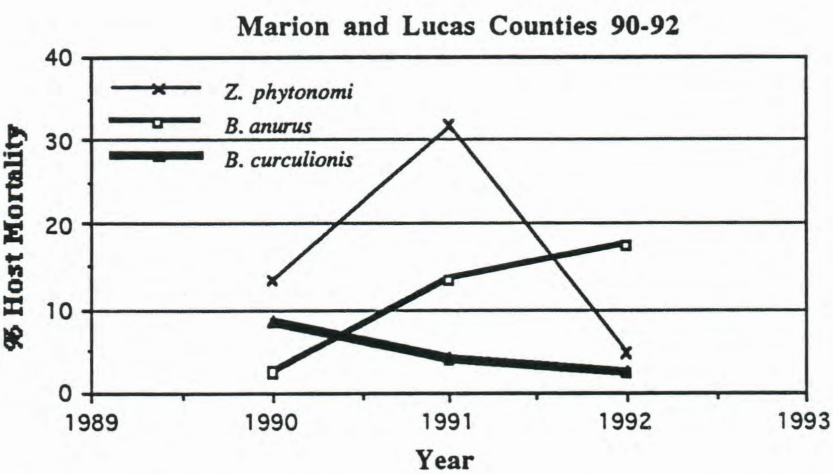

Fig. 1. Mean Seasonal incidence of *Z. phytonomi*, *B. anurus*, and *B. curculionis* on *H. postica* larvae at Marion and Lucas Counties, 1990-1992

From Giles, 1992.

Table 2. Rainfall averages, rainfall days, first incidence of, and peak mortality by *Z. phytonomi* at Story, Polk, Marion, and Lucas counties during the presence of *H. postica* larvae on first harvest alfalfa, 1990-1992

Year / Location	Mean rainfall[a] (1991-92) (mm/day)	Average rainfall[b] (1951-80) (mm/day)	Rainfall days[c]	*Zoophthora phytonomi* 1st incidence (DD > 9°C)[d]	*Zoophthora phytonomi* Peak mortality[e]
1990					
Marion Co.	4.5 mm	3.2 mm	21/49	190 DD	52.4%
Lucas Co.	4.1 mm	3.1 mm	19/42	212 DD	34.6%
1991					
Story Co.	3.6 mm	3.2 mm	14/28	169 DD	83.9%
Polk Co.	6.5 mm	3.0 mm	18/35	168 DD	92.8%
Marion Co.	7.0 mm	3.2 mm	25/42	207 DD	85.3%
Lucas Co.	5.7 mm	3.1 mm	25/42	187 DD	93.3%
1992					
Story Co.	0.7 mm	3.2 mm	10/35	292 DD	75.0%
Polk Co.	0.7 mm	3.0 mm	6/42	293 DD	32.2%
Marion Co.	1.4 mm	3.2 mm	9/42	378 DD	2.2%
Lucas Co.	3.4 mm	3.1 mm	17/35	251 DD	28.4%

[a] Mean rainfall is the calculated daily rainfall from first detection of *H. postica* larvae until harvest, and/or sampling termination at each sampling site in 1990, 1991 and 1992.

[b] Average rainfall is the average daily rainfall from 1 April to 31 May, 1951-1980 (NOAA report, Climatology of U.S., #81, Iowa 1951-80).

[c] Rainfall days is the number of days that measurable rainfall was recorded, during the period when *H. postica* larvae were detected at each sampling site, over the total number of days that *H. postica* larvae were collected.

[d] Degree-day accumulation after January 1, above a base 9°C.

[e] Peak percentage mortality at each sampling site, each year, based upon the number of reared *H. postica* larvae that died from *Z. phytonomi*, divided by the total number of larvae reared on one sampling date.

From Giles, 1992.

study; five were associated with above average rainfall (Table 2). During 1991, epizootics of *Z. phytonomi* in Story, Polk, Marion, and Lucas Counties killed between 15 and 61% of field collected *H. postica* larvae (Table 1).

Mortality of *H. postica* larvae from *Z. phytonomi* was lower during the dry spring in 1992 compared to 1991 (Table 1; Table 2). For example, *Z. phytonomi* was not confirmed in the sampled northeastern Iowa counties in 1992. Additionally, mortality attributable to *Z. phytonomi* decreased in Marion County from 49% to 1% (Table 1). In 1990 and 1992 at Lucas County, rainfall levels were above normal, however, epizootics were not observed because fields were cut during the initial progression of disease. In 1992, the alfalfa field at Polk County also was cut during the initial progression of disease. An epizootic, possibly triggered by dew formation, was observed at Story County in 1992 when rainfall averaged 0.7 mm per day (Table 2).

In Kentucky, a host density of 1.7 larvae per stem was required for an epizootic to occur (Brown & Nordin 1982). In contrast, an epizootic of *Z. phytonomi* was observed on *H. postica* densities of 0.9 larvae per stem in Ontario when rainfall during the first three weeks of June exceeded 4.3 mm day (Harcourt et al. 1990). In 1990, an epizootic was observed at Marion County when larval densities peaked at 0.84 larvae per stem and rainfall averaged 4.5 mm per day (Table 2). In 1991, when rainfall levels were above average we observed epizootics at each sampling site on larval densities of less than 1.3 larvae per stem (Story 1.26 ± 0.22, Polk 1.0 ± 0.25, Marion 0.77 ± 0.16, Lucas 0.65 ± 0.17) (Table 2). The only epizootic in 1992 occurred in Story County at densities of 1.60 ± 0.18 larvae per stem during very low rainfall.

Parasitoid-Pathogen interactions

It appear that epizootics of *Z. phytonomi* may disrupt the stability of the *H. postica* - parasitoid ecosystem and result in sporadic pest outbreaks. Alternatively, low rainfall may be the disruptive force in a stable *H. postica* -pathogen system. After two years of below-average rainfall in southern Iowa (Iowa Climate Review 1988, 1989), *H. postica* densities increased to economically damaging levels in 1989 and 1990. Above-average rainfall in 1990 and 1991 promoted epizootics of *Z. phytonomi*, which reduced *H. postica* populations to sub-economic levels. Rainfall in 1992 was below average in Iowa, and mortality by *Z. phytonomi* declined without an increase in larval parasitism. Because larval parasitoids are negatively affected by *Z. phytonomi* and may lag behind *H. postica* population increases (Harcourt & Guppy 1991), the potential for a 1993 outbreak existed. In 1993, more than 2000 acres of alfalfa in southeastern Iowa were treated with insecticides to reduce *H. postica* densities (Marlin Rice, personal communication).

The impact of *Z. phytonomi* is greater on *B. curculionis* because this wasp attacks younger *H. postica* instars, thus the host and developing parasitoid are exposed to *Z. phytonomi* for extended time periods. In contrast, *B. anurus* lays eggs in later *H. postica* instars that have a greater probability of avoiding *Z. phytonomi*, because they require less time to reach the adult stage. From 1990-1992, *B. curculionis* declined in Marion and Lucas Counties, whereas *B. anurus* and total percentage parasitism increased. (Table 1; Fig 1). The change in densities of *B. curculionis* and *B. anurus* occurred during and after epizootics of *Z. phytonomi* in 1991.

Predators of Alfalfa Weevil Larvae

The most abundant predatory species collected was *C. maculata* which peaked at 104 adults per 100 sweeps in Polk County (15 May, 1992). Adult *C. maculata* outnumbered all other coccinellid predators combined in 1991 (95% of all adult coccinellids collected) and 1992 (80%). Other coccinellid (Lady Beetles) adults were rarely found in 1991, peaking at less than 2 adults per 100 sweeps for all species combined. In 1992, *Hippodamia convergens* (Guerin) numbers peaked at 1 adult per 6 sweeps (Lucas County, 5 May). *Coccinella septempunctata* (L.) numbers peaked at 1 adult per 15 sweeps (Story County, 19 May), while *H. tredecimpunctata* (Say) peaked at 1 adult per 19 sweeps (Story County, 19 May). Totals for hemipteran predators (Nabids and Stinkbugs) were similar in 1991 and 1992. Hemipteran densities in sweep samples were low (relative to prey densities) each spring, with a peak of 1 individual per 9 sweeps (Story County 1992).

Adult *C. maculata* are highly correlated to both *H. postica* larvae and *A. pisum* in the alfalfa canopy which indicates an aggregative response to spatial variation in the densities of both prey species. Because of the high correlation between prey it is difficult to determine whether *C. maculata* adults aggregate to *H. postica* populations or to *A. pisum* populations. Aggregation most likely occurs to both prey species, with rate differences attributable to prey density differences (Price 1984). It is important to note, however, that *C. maculata* adults do show a consistent pattern of aggregation to *H. postica* larval densities in Iowa alfalfa fields even when *A. pisum* densities were low.

The abundance of *C. maculata* in Iowa alfalfa fields may be attributable to its aggregative behavior to densities of *H. postica* larvae and *A. pisum* in alfalfa (Giles et al. in press). Because *C. maculata* tends to remain in alfalfa fields at low prey densities it may be a more effective forager or less preferential, compared to other predators, when seeking prey in alfalfa.

Summary and Future Directions

Z. phytonomi infected populations of *Hypera postica* larvae in northeastern Iowa in 1991, and in central and southcentral Iowa in 1990, 1991, and 1992. Six epizootics (>50% host infection) were observed in central and southcentral Iowa during this three year study; five were associated with above average rainfall. In 1992, enzootics (<50% host infection) of *Z. phytonomi* occurred during Late May and Early June on declining populations of *H. postica* larvae at three sites. An epizootic occurred in central Iowa despite below average rainfall.

Parasitization of *H. postica* larvae in Iowa by *B. curculionis* and *B. anurus* ranged from 2 to 28% in 1990, 1991, and 1992. *B. curculionis* parasitization rates at two southern Iowa locations declined during epizootics of *Z. phytonomi* each year, suggesting a negative effect of *Z. phytonomi* on this larval parasitoid. *B. anurus* became the most abundant larval parasitoid at the two locations in southern Iowa following epizootics of *Z. phytonomi.*

Adult *C. maculata* were the most abundant predators found in alfalfa from 16 April to 7 June (1991-1992). Adult *C. maculata* numbers peaked in 1992 at more than one per sweep in Polk County (15 May). *C. maculata* adults are highly correlated to varying spatial densities of *H. postica* larvae and pea aphids, *A. pisum* .

Even though *Z. phytonomi* has been documented throughout much of the United States, many aspects of the pathogen and its biology have been not been determined. Understanding the activity of the fungus in early spring is critical for the development of manipulative techniques designed to initiate epizootics in the field. This basic ecological information can be used to create appropriate microhabitats which favor the spread of the fungus on early spring populations of alfalfa weevil larvae. For example, early spring strip harvesting, reduced rates of insecticides, microbial insecticides, and inoculative host and pathogen releases could initiate epizootics earlier in the season and reduce larval populations below economic levels. Early spring strip harvesting would concentrate larvae in appropriate microhabitats (within the cut strip) for the initiation and spread of disease (to uncut alfalfa) (Brown et al. 1986). Also, early strip harvesting would allow much of the field to grow to maturity, conserving natural enemies (Summers et al. 1981) and increasing yields (versus early harvest of the entire field). Reduced rates of conventional and microbial insecticides, aimed at reducing early stage larval populations to below 2 larvae per stem (Wintersteen et al. 1992), could dislodge large numbers of larvae, which could serve as host cadavers for the early initiation and spread of disease. Early epizootics created by inoculative releases of the fungus or sentinel larvae (Infected and non-infected) could serve as local foci to initiate cycling of the fungus. With the knowledge gained during the previous three years, we have focused our future research efforts on these techniques for management of the alfalfa weevil in Iowa.

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